



Lateralization of spatial rather than temporal attention underlies the left hemifield advantage in rapid serial visual presentation

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ABSTRACT

In bilateral rapid serial visual presentation (RSVP), the second of two targets, T1 and T2, is better identified in the left visual field (LVF) than in the right visual field (RVF). This LVF advantage may reflect hemispheric asymmetry in temporal attention or/and in spatial orienting of attention. Participants performed two tasks: the “standard” bilateral RSVP task (Exp.1) and its unilateral variant (Exp.1 & 2). In the bilateral task, spatial location was uncertain, thus target identification involved stimulus-driven spatial orienting. In the unilateral task, the targets were presented block-wise in the LVF or RVF only, such that no spatial orienting was needed for target identification. Temporal attention was manipulated in both tasks by varying the T1-T2 lag. The results showed that the LVF advantage disappeared when involvement of stimulus-driven spatial orienting was eliminated, whereas the manipulation of temporal attention had no effect on the asymmetry. In conclusion, the results do not support the hypothesis of hemispheric asymmetry in temporal attention, and provide further evidence that the LVF advantage reflects right hemisphere predominance in stimulus-driven orienting of spatial attention. These conclusions fit evidence that temporal attention is implemented by bilateral parietal areas and spatial attention by the right-lateralized ventral frontoparietal network.

1. Introduction

1.1. LVF advantage in bilateral RSVP

Holländer, Corballis, and Hamm (2005) utilized a bilateral variant of the rapid serial visual presentation (RSVP) paradigm (Broadbent & Broadbent, 1987) to study lateralization of attention. This bilateral RSVP task consisted of two simultaneous streams of distractors, presented in the left and right visual fields (LVF & RVF), and two targets, T1 and T2, occurring in either visual field (VF) with 50/50 probability and with varying T1-T2 lags (ranging from 100 to 800 ms). Holländer et al. (2005) obtained a striking LVF advantage in T2 identification: left T2s were identified up to 30% better than right T2s, which contrasts with small VF effect sizes usually observed in other tasks (see Hellige, Laeng, & Michimata, 2010 for review). This LVF advantage has been replicated repeatedly (Asanowicz, Śmigasiewicz, & Verleger, 2013; Holländer, Hausmann, Hamm, & Corballis, 2005; Kranczoch, Lindig, & Hausmann, 2016; Verleger, Dittmer, & Śmigasiewicz, 2013; Verleger et al., 2009; Verleger, Śmigasiewicz, & Möller, 2011; Śmigasiewicz et al., 2010) and

evidence has been brought forward that it reflects lateralization of exogenously triggered spatial attention (Śmigasiewicz, Asanowicz, Westphal, & Verleger, 2015; Śmigasiewicz, Westphal, & Verleger, 2017). In the present study, we investigated whether there is also a contribution of hemispheric lateralization of temporal attention to this LVF advantage, as originally proposed by Holländer et al. (2005).

1.2. Right hemisphere advantage in temporal attention

We define temporal attention as a process of transient temporal modulations, both enhancements and suppressions, of information processing by a mechanism of attentional gating or filtering, which allows to select and single out relevant events from a continuous flow of perceptual information (Bowman & Wyble, 2007; Olivers & Meeter, 2008). The need for selective attention arises from resource limitations; information processing must be selective when demands exceed capacity of perceptual or cognitive systems (Lavie & Dalton, 2014; Mozer & Sittton, 1998). In the RSVP tasks, demands for temporal attention are largest when T2 occurs within 200–500 ms after T1 (i.e., with a short T1-T2 lag) and the two targets are separated by at least one

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distractor, i.e., during a period of visual constraints known as the attentional blink (Raymond, Shapiro, & Arnell, 1992). The LVF advantage in T2 identification was interpreted by Holländer et al. (2005) in this line, as evidence that “the right hemisphere is superior in performing an attentional blink task, and therefore in the modulation of temporal attention” (p.39), and they concluded that temporal attention is subserved mainly by the right hemisphere. It is often assumed that the left hemisphere (LH), rather than the right hemisphere (RH), is specialized in temporal processing of visual information (Nicholls, 1996; Nicholls, Gora, & Stough, 2002; Okubo & Nicholls, 2005). Nonetheless, there are results suggesting that temporal attention may indeed be lateralized to the RH. Decoding of temporal order of visual events or determining when exactly an event occurs in a stream of stimuli is performed better in the LVF than in the RVF (Funnell, Corballis, & Gazzaniga, 2003), also in bilateral RSVP (Matthews & Welch, 2015; Matthews, Welch, Festa, & Clement, 2013), and these asymmetries may reflect lateralization of temporal attention, as temporal attention is a major factor determining which perceptual event has priority and which information enters to consciousness more quickly (Hilkenmeier, Olivers, & Scharlau, 2012). Battelli, Pascual-Leone, and Cavanagh (2007) have suggested that temporal/transient attention is controlled in both VFs by the right inferior parietal lobe (IPL), a crucial node for the processing of the temporal dimension (termed by those authors the ‘when’ pathway). Furthermore, the RH advantage in temporal processing is more likely to become evident when a task requires sustained temporal monitoring (Okubo & Nicholls, 2008; Whitehead, 1991), which is the case in the RSVP task. Finally, there is evidence from lesion (Husain, Shapiro, Martin, & Kennard, 1997), transcranial magnetic stimulation or TMS (Cooper, Humphreys, Hulleman, Praamstra, & Georgeson, 2004), and fMRI imaging studies (Marois, Chun, & Gore, 2000) suggesting a critical role of the right intraparietal sulcus (IPS) in target selection during the attentional blink period. Thus far, however, the hypothesis that the LVF advantage in the RSVP task reflects lateralization of temporal attention has not been further pursued and there is therefore no experimental evidence available.

1.3. Right hemisphere advantage in spatial attention

The bilateral RSVP task, in addition to uncertainty of the targets’ temporal locations (lag variation) which is standard for this paradigm, adds uncertainty of their spatial locations (VF variation). Thus, also spatial attention is engaged in the task of T2 identification. A large number of studies has shown that spatial orienting of attention to behaviorally relevant stimuli occurring at unpredictable, uncertain, or uncued locations is controlled by a right-lateralized ventral frontoparietal network comprising the right temporoparietal junction (TPJ) and the right ventral frontal cortex (see Corbetta, Patel, & Shulman, 2008; Singh-Curry & Husain, 2009, for reviews). More recent studies have suggested that this network is also related to the transition from monitoring to target detection (Shulman & Corbetta, 2012). These two functions are crucial for successful T2 identification in bilateral RSVP. The LVF advantage may therefore be caused by this RH predominance in stimulus-driven orienting of spatial attention, rather than lateralization of temporal attention. We examined this hypothesis in our recent study (Śmigajewicz et al., 2015) varying involvement of spatial orienting in T2 identification by displaying spatially valid, invalid, or neutral exogenous cues before T2 onset. The results showed that the LVF advantage increased with increased involvement of spatial attention in target identification (invalid cue condition) and was almost abolished with decreased involvement of spatial attention (valid cue condition), suggesting that the asymmetry may indeed be caused by lateralization of stimulus-driven spatial orienting. A follow-up study has confirmed these findings (Śmigajewicz, Westphal, et al., 2017). However, two other studies showed that the LVF advantage can also be significantly reduced, but not abolished, by endogenous spatial cueing (Śmigajewicz, Hasan, & Verleger, 2017; Verleger et al., 2009, Exp.2). A

possible reason of this difference in cueing effects is that while the endogenous cueing signaled T2’s spatial location only (thereby only reducing the asymmetry), the exogenous cueing actually signaled both the spatial and temporal locations of T2, as cues popped out always right before T2 onset (and abolished the asymmetry). This again hints at temporal attention as one of possible causes of the asymmetry. Plausibly, when only spatial location is known before T2 onset, temporal attention still needs to be engaged in T2 identification, thus there is still the LVF advantage, in line with the hypothesis of lateralization of temporal attention. However, when both spatial and temporal locations of T2 are known in advance, the asymmetry is abolished, because then there is no need for further involvement of attentional resources in T2 identification. In conclusion, the LVF advantage may be produced by combined impact of lateralization of both spatial and temporal attention.

1.4. Present study

We conducted two RSVP experiments aiming to further investigate whether the attentional blink/temporal attention is lateralized, and whether the LVF advantage in T2 identification can be explained by lateralization of temporal or/and spatial attention. In Exp.1, participants performed two RSVP tasks: the “standard” bilateral task (Holländer et al., 2005; Verleger et al., 2011), and its modified version, a unilateral task. Involvement of temporal attention was varied within the tasks by the trial-by-trial lag manipulation, from least (lag 8) to moderate (lag 4) and to most (lag 2) involvement. Involvement of spatial attention was varied between the tasks. In the bilateral task, spatial locations of the targets were uncertain due to trial-by-trial manipulation of T1/T2 VFs (LVF or RVF), so that participants did not know where the targets would occur, and T2 identification involved exogenous spatial orienting of attention triggered by T2 onsets. In the unilateral task, this spatial uncertainty was removed. The two lateral streams of distractors were presented simultaneously in the two VFs, like in the bilateral task, and the two targets, T1 and T2, were presented in one stream only, in the LVF or in the RVF (block-wise), so that participants did know in advance where both targets would occur. Therefore, a steady spatial focus was kept on the target stream endogenously during the whole trial, whereas the need for exogenous spatial orienting was eliminated. (Similar methods of presentation of lateral targets at one VF block-wise while keeping central fixation have been used before in other experimental paradigms, e.g., Bisiacchi et al., 1994; Slagter, Prinssen, Reteig, & Mazaheri, 2016). In Exp.2, we utilized a longer version of the unilateral task, aiming to confirm the results of the unilateral task from Exp.1, which were new findings, unlike the results of the bilateral task.

If the LVF advantage is caused by lateralization of temporal attention, the asymmetry should be a function of the degree of involvement of temporal attention. Thus, the shorter is the lag, the larger should be the LVF advantage. Assuming no additional influence of spatial attention, the effects of lag on the LVF advantage should be similar in the unilateral and bilateral tasks, and no LVF advantage should be found at lags beyond the attentional blink (i.e., lag 8; T2 identification is easy, which diminishes the need for temporal attention). However, since previous studies have suggested that at least part of this asymmetry may be caused by lateralization of spatial attention, the LVF advantage may be generally larger in the bilateral task than in the unilateral task due to additive effects of temporal and spatial attention, and be present also in the no-blink lag 8 condition of the unilateral task. Alternatively, if caused solely by lateralization of exogenous orienting of spatial attention, the LVF advantage should be present, as usual, in the bilateral task, in which spatial attention is necessary for T2 identification, but should be absent in the unilateral task, in which spatial uncertainty, and thereby the need for exogenous orienting, is removed. As a third option, if caused by lateralization of endogenous spatial attention, the LVF advantage should even increase in the unilateral task, where a steady,

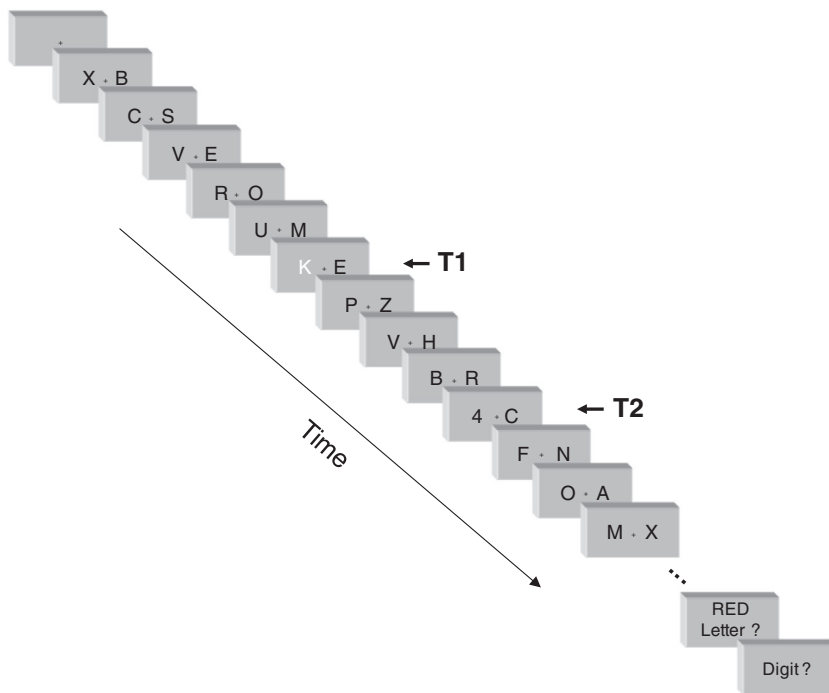


Fig. 1. Sequence of events in a trial. The example shows LVF T1 at 6th position followed by LVF T2 at lag 4. See Section 2.1 for details. Red color is replaced here by white. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

controlled focus of attention is useful, compared to the bilateral task.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Twenty right-handed participants (12 females) took part in the first experiment. Their mean age was 24.8 years ($SD = 6.5$) and mean Edinburgh Inventory (Oldfield, 1971) score was 94.3 ($SD = 7.8$). All participants had normal or corrected-to-normal vision, reported normal color vision, and no history of neurological disorders. Informed written consent was obtained before the experiment. 20 € were paid for participation.

2.1.2. Stimuli, apparatus, and procedure

Participants performed one RSVP task with targets presented unilaterally (unilateral task), and another RSVP task with targets presented bilaterally (bilateral task).

Unilateral task. The task is illustrated in Fig. 1. Two simultaneous streams of distractor stimuli (Latin letters) were presented in the left and right visual field, with two targets, T1 and T2, embedded in either the left or right stream. Both targets were present and had to be identified in each trial. Side of the targets changed block-wise, and T2 occurred always on the same side as T1. T1 was preceded by five, seven, or nine pairs of distractors, and T1-T2 lags amounted to 240 ms (lag 2), 480 ms (lag 4), or 960 ms (lag 8). Thus, while participants always knew where the two targets would occur, they did not know when this would happen. T2 was always followed by three distractor pairs. Therefore, trial length varied between 11 pairs of stimuli (when T1 came at the 6th position and T1-T2 lag was 2) and 21 pairs of stimuli (when T1 came at the 10th position and T1-T2 lag was 8). At the end of each trial, first a T1 and then a T2 response screen appeared, displaying all six possible targets and the instruction to press the appropriate key on the computer keyboard. The next trial started automatically after the response on T2. Each trial started with a fixation period of 800 ms. Each pair of stimuli was presented for 120 ms, immediately followed by the next frame, without inter-stimulus intervals. The fixation point was present on the screen throughout the whole trial.

Bilateral task. The bilateral task was similar to the ‘standard’ bilateral RSVP task (Holländer et al., 2005; Verleger et al., 2011). T1 would occur either in the LVF or RVF with 50/50 probability (randomized within blocks) and T2 could occur either on the same side as T1 or on the other side also with 50/50 probability. Therefore, participants not only did not know when the two targets would occur, like in the unilateral task, but also did not know where the targets would occur. All other parameters were identical in both tasks.

Stimuli. Distractor stimuli consisted of black Latin letters (of a set of 24), T1 was a red Latin letter (D, F, G, J, K, or L) and T2 was a black Arabic digit (ranging from 1 to 6). Targets were randomly selected from the target sets, and background stimuli were randomly selected with replacement (with a restriction against immediate repetition and against identical letters simultaneously in the two streams). Distractor stimuli, T2s (1 cd/m^2) and red T1s (24 cd/m^2) were presented on the white background (120 cd/m^2) of a 17" screen driven with 100 Hz, at about 1 meter from participants' eyes. The font *Helvetica* was used for letters and digits. Fixation was marked by a small red cross ($0.2^\circ, 0.2^\circ$) at the center of the screen. Stimuli were about 8.5 mm wide and 11 mm high ($0.5^\circ, 0.6^\circ$) with their inner edge about 14 mm from fixation (0.7°).

Procedure. Before each task, participants were given written and then verbal instructions, and performed some practice trials with stimuli presented in slow motion (500 ms display time for each pair) and then in normal speed (120 ms for each pair). Participants performed two blocks of one task and then two blocks of the other task. In the unilateral task, blocks differed by the targets' VF. Each task consisted of 360 trials (60 repetitions of each VF/lag condition, 180 trials per block). The experimental session lasted up to one hour and fifteen minutes. Presentation software was used for experimental control (Neurobehavioral Systems Inc., Albany, CA).

Participants were carefully instructed to keep central fixation throughout the whole trial, until onset of the response screen, while focusing their covert attention on the target VF from the beginning of each trial. They also read written instructions with an explanation of why proper fixation is important. Fixation was controlled with a remote infrared eye tracker (600 series bin-ocular, Eyegaze LC Technologies, Fairfax, VA) and online feedback by software (Interactive Minds, Dresden, Germany), which communicated with the Presentation program. In case of a deviation of more than 6 mm from vertical midline at

Table 1
Percentages of correct identification of targets in Exp.1.

| | Task | Lag | VF | Mean | SD |
|----|---|-----|-----|------|----|
| T1 | Unilateral task | 2 | LVF | 76 | 17 |
| | | | RVF | 83 | 12 |
| | | 4 | LVF | 77 | 16 |
| | | | RVF | 84 | 12 |
| | | 8 | LVF | 77 | 17 |
| | | | RVF | 83 | 14 |
| | Bilateral task | 2 | LVF | 78 | 14 |
| | | | RVF | 82 | 11 |
| | | 4 | LVF | 79 | 14 |
| | | | RVF | 81 | 13 |
| | | 8 | LVF | 77 | 16 |
| | | | RVF | 82 | 15 |
| T2 | Unilateral task | 2 | LVF | 76 | 14 |
| | | | RVF | 73 | 15 |
| | | 4 | LVF | 81 | 13 |
| | | | RVF | 79 | 13 |
| | | 8 | LVF | 93 | 8 |
| | | | RVF | 90 | 8 |
| | Bilateral task, T1 and T2 in the same VF | 2 | LVF | 84 | 13 |
| | | | RVF | 73 | 16 |
| | | 4 | LVF | 86 | 15 |
| | | | RVF | 74 | 16 |
| | | 8 | LVF | 94 | 7 |
| | | | RVF | 79 | 21 |
| | Bilateral task, T1 and T2 in different VFs | 2 | LVF | 64 | 20 |
| | | | RVF | 40 | 21 |
| | | 4 | LVF | 84 | 12 |
| | | | RVF | 66 | 23 |
| | | 8 | LVF | 96 | 6 |
| | | | RVF | 82 | 15 |

trial onset, a red exclamation mark was presented at midline, inducing shifts of gaze back to fixation.

2.1.3. Data analysis

Percentage of correct T1 identification was calculated out of all trials, and percentage of T2 identification was calculated from trials in which both T1 and T2 were correctly identified out of all trials in which T1 was correctly identified (T2|T1). T1 accuracy rates were analyzed by $3 \times 2 \times 2$ analyses of variance (ANOVAs) with Lag (2, 4, 8), VF (LVF, RVF), and Task (unilateral, bilateral) as within-subject factors. T2 accuracy rates were analyzed by distinguishing between bilateral task conditions with T1 and T2 in the same and in different VFs, by means of a $3 \times 2 \times 3$ ANOVA with Lag (2, 4, 8), VF (LVF, RVF), and Task (unilateral, bilateral/same side [SS], bilateral/different sides [DS]) as within subject factors. Degrees of freedom were corrected by Greenhouse-Geisser's ϵ when repeated-measure factors had more than two levels.

2.2. Results

Target identification rates are compiled in Table 1 and depicted in Fig. 2 (left and middle parts of both panels).

2.2.1. T1 identification

The overall T1 identification rate was 80% (SD = 14%). T1 was better identified in the right than the left VF (main effect of VF $F_{1,19} = 11.3$, $p = 0.003$), and the VF \times Task interaction was marginally significant, $F_{1,19} = 3.8$, $p = 0.065$, reflecting a larger RH advantage in the unilateral task (LVF: 76% vs. RVF: 83%, $F_{1,19} = 13.2$, $p = 0.002$) than in the bilateral task (LVF: 78% vs. RVF: 81%, $F_{1,19} = 4.9$, $p = 0.040$). Other effects were not significant, $F_s < 1.0$.

2.2.2. T2 identification

Overall T2 identification accuracy was 79% (SD = 13%). The ANOVA showed significant main effects of Lag, $F_{2,38} = 60.9$, $p < 0.001$, with accuracy increasing from lag 2 to lag 8, and of VF, $F_{1,19} = 34.2$, $p < 0.001$, with better identification in the left than the right VF. Importantly, these effects depended on the task: There was a main effect of Task, $F_{2,38} = 17.3$, $p < 0.001$, and significant interactions Lag \times Task, $F_{4,76} = 27.4$, $p < 0.001$, and VF \times Task, $F_{2,38} = 10.5$, $p < 0.001$. Other interactions were not significant, $F \leq 1.6$.

Pairwise comparisons between two of the three task conditions, to localize the Task effects, showed that accuracy in the different side (DS) condition of the bilateral task (72%) was lower than in the unilateral task (82%), $F_{1,19} = 26.4$, $p < 0.001$, and in the same side (SS) condition of the bilateral task (81%), $F_{1,19} = 23.4$, $p < 0.001$, while unilateral task and the SS condition of the bilateral task did not differ, $F < 1.0$, n.s. Resolving the Lag \times Task interaction, the Lag effect was largest in the DS condition of the bilateral task ($F_{2,38} = 77.3$, $p = 0.001$, linear trend: $F_{1,19} = 107.8$, $p < 0.001$), intermediate in the unilateral task ($F_{2,38} = 43.5$, $p < 0.001$, linear trend: $F_{1,19} = 64.0$, $p < 0.001$), and smallest in the SS condition of the bilateral task ($F_{2,38} = 6.1$, $p = 0.001$, linear trend: $F_{1,19} = 6.3$, $p = 0.02$). (Lag \times Task interactions in pair-wise comparisons: bilateral/DS vs. unilateral $F_{2,38} = 33.8$, $p = 0.02$, unilateral vs. bilateral/SS $F_{2,38} = 4.6$, $p = 0.02$, and bilateral/DS vs. bilateral/SS $F_{2,38} = 39.8$, $p = 0.02$).

Of importance, when resolving the VF \times Task interaction, a significant VF effect was found only in the bilateral task. Although there was a small trend for the LVF advantage in the unilateral task, consistent across the lags (see Fig. 2), this effect did not reach the significance level, $F = 1.1$, n.s. In contrast, the LVF advantage was found in both the SS and DS conditions of the bilateral task: LVF vs. RVF in SS 87% vs. 75%, $F_{1,19} = 25.3$, $p < 0.001$, and in DS 81% vs. 63%, $F_{1,19} = 39.9$, $p < 0.001$. Pairwise comparisons between tasks of the VF \times Task interaction showed that this LVF advantage was marginally larger in the DS than SS condition, $F_{1,19} = 3.9$, $p = 0.06$, and in either case larger than in the unilateral task: bilateral SS vs. unilateral $F_{1,19} = 6.8$, $p = 0.017$, and bilateral DS vs. unilateral $F_{1,19} = 19.7$, $p < 0.001$.

3. Experiment 2

In Exp.1, the LVF advantage was found to be present in the bilateral task, as usual, and to be abolished in the unilateral task. While this result of the bilateral task has been repeatedly observed in previous RSVP studies, the result of the unilateral task was new. Moreover, a small non-significant trend for a LVF advantage in T2 identification was still present in the unilateral task, suggesting that the lack of significance might be due to insufficient statistical power. Therefore, the second experiment aimed to confirm the results of the unilateral task.

3.1. Methods

Only differences from Experiment 1 will be described.

3.1.1. Participants

Twenty-one right-handed participants took part in Experiment 2. One participant was rejected due to systematic eye movements toward the target streams. Mean age of the remaining 20 participants (13 females) was 23.1 years (SD 3.1) and their mean Edinburgh Inventory (Oldfield, 1971) score was 95.0 (SD 7.7).

3.1.2. Stimuli, apparatus, and procedure

Only the unilateral task was performed. Three minor changes were introduced to the task: the overall number of trials was increased to 576 trials (72 repetitions of each experimental condition, 288 trials per VF),

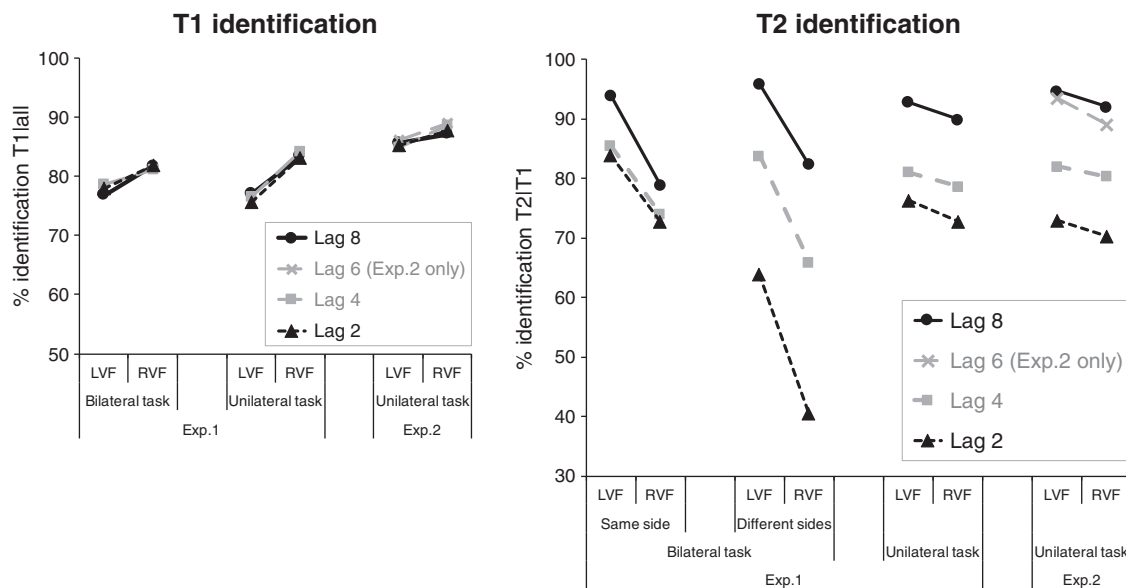


Fig. 2. Identification rates of T1 (left panel) and T2 (right panel) in the two experiments (Exp.1 and Exp.2). The T1 rates of the bilateral task (Exp.1) are pooled across the T1-T2 side change conditions. LVF and RVF denotes left and right visual fields.

stimuli were presented for 130 ms (cf. Verleger et al., 2011, 2013) instead of 120 ms, and Lag 6 was added to have equal differences between lags, so that T1-T2 lags amounted to 260 ms (lag 2), 520 ms (lag 4), 780 ms (lag 6), or 1040 ms (lag 8). After a practice session, participants performed four blocks of the task (144 trials per block).

3.1.3. Data analysis

T1 and T2 identification rates were calculated as in Exp.1 and submitted to 4×2 repeated measure ANOVAs with Lag (2, 4, 6, 8) and Visual Field (LVF, RVF) as within-subject factors.

3.2. Results¹

Target identification rates are compiled in Table 2 and depicted in Fig. 2 (right parts of both panels).

3.2.1. T1 identification

The overall T1 identification rate was 87% (SD = 13%) (7% higher than in the unilateral task of Exp.1, but this difference was not significant, $F_{1,38} = 2.4$, $p = 0.13$). Only the main effect of VF was significant, $F_{1,19} = 6.6$, $p = 0.02$, showing a 3% RVF advantage (other effects: $F_s < 1.0$, n.s.).

3.2.2. T2 identification

T2 was identified with 84% accuracy (SD = 14%). The main effect of Lag was significant, $F_{3,57} = 25.8$, $p < 0.001$, showing a typical attentional blink effect (accuracy from lag 2 to 8, respectively: 71%, 81%, 91%, 93%, linear trend: $F_{1,19} = 41.4$, $p < 0.001$). Accuracies at all shorter lags were significantly lower than in the baseline lag 8 condition (Lag 2 vs. Lag 8: $F_{1,19} = 38.8$, $p < 0.001$; Lag 4 vs. Lag 8: $F_{1,19} = 19.2$, $p < 0.001$; Lag 6 vs. Lag 8: $F_{1,19} = 3.9$, $p = 0.06$). Of importance, although there was a trend for a LVF advantage, 86% vs. 83%, the main effect of VF did not reach the significance level, $F_{1,19} = 3.5$, $p = 0.08$, nor was the Lag \times VF interaction significant, $F < 1.0$, indicating no impact of lag variation on the VF asymmetry. Therefore, the results of Exp.2 are fully consistent with Exp.1.

Because this non-significant trend for a LVF advantage was present

Table 2

Percentages of correct identification of targets in Exp.2.

| | Lag | VF | Mean | SD |
|----|-----|-----|------|----|
| T1 | 2 | LVF | 85 | 13 |
| | | RVF | 88 | 13 |
| | 4 | LVF | 85 | 15 |
| | | RVF | 89 | 13 |
| | 6 | LVF | 86 | 14 |
| | | RVF | 89 | 11 |
| | 8 | LVF | 86 | 14 |
| | | RVF | 87 | 14 |
| T2 | 2 | LVF | 73 | 17 |
| | | RVF | 70 | 23 |
| | 4 | LVF | 82 | 16 |
| | | RVF | 80 | 21 |
| | 6 | LVF | 93 | 9 |
| | | RVF | 89 | 11 |
| | 8 | LVF | 95 | 9 |
| | | RVF | 92 | 9 |

consistently in both experiments, it appeared possible that with larger statistical power the effect would reach the significance level. However, an omnibus ANOVA on the data from both experiments pooled together (omitting lag 6) still showed no significant main effect of VF, $F_{1,39} = 2.6$, $p = 0.11$, and no significant VF \times Lag interaction, $F < 1.0$, as well as no significant effects of Experiment, $F_s < 1.0$.

4. Discussion

4.1. Summary of results

In the unilateral task (Exp.1 and 2), T1 was better identified in the RVF than in the LVF, whereas the difference between VFs in T2 identification was found to be insignificant. T1-T2 lag manipulation produced the typical attentional blink effect: the shorter the lag, the lower was T2 identification rate. This lag effect did not interact with VF. In the bilateral task (Exp.1), T1 was also identified better in the RVF than in the LVF. In contrast, T2 was identified markedly better in the LVF than in the RVF, replicating once again the repeatedly observed LVF advantage (Asanowicz et al., 2013; Holländer et al., 2005; Kranczioch et al., 2016; Verleger et al., 2009; Verleger et al., 2011; Verleger et al.,

¹ These data were already briefly reported by Asanowicz, Verleger, Kruse, Beier, and Śmigajewicz (2017, Appendix A2) where the focus was on distractor-evoked event-related EEG potentials.

2013; Śmigasiewicz et al., 2010). This LVF advantage tended to be smaller in trials with T1 and T2 in the same VF than in trials with T1 and T2 in different VFs, and was not affected by the lag manipulation. In summary, first, the LVF advantage was found as usual when target spatial location was uncertain, and was abolished by removing this spatial uncertainty; second, increasing involvement of temporal attention by reduction of T1-T2 lags did not have impact on any of the VF effects.

The obtained results are in line with the hypothesis that the LVF advantage in T2 identification reflects a LVF advantage in stimulus-driven spatial attention, possibly due to right hemisphere predominance, and contradict the hypothesis that the LVF advantage in T2 identification reflects lateralization of the attentional blink or some general right-hemisphere superiority in temporal attention. Nor did the hypothesis of lateralization of endogenous spatial orienting gain any support, because by its being insignificant in the unilateral task, the LVF advantage was far off from being larger in the unilateral than the bilateral task. Also, the observed effect of uncertainty/task on the LVF advantage cannot be alternatively explained by increased task difficulty or attentional load in the bilateral task, because: (1) there was no difference in overall T1 accuracy between the tasks in Exp.1, (2) there was no difference in overall T2 accuracy between the unilateral task and the same side (SS) condition of the bilateral task in Exp.1, while there was a significant difference in VF effects on T2 between these conditions, (3) although the unilateral task in Exp.2 was slightly easier than in Exp.1 (though insignificantly) due to longer stimulus presentations (130 vs. 120 ms), no differences were found in T2 VF effects. Lastly, the RVF advantage in T1 identification seems to reflect the well-known left hemisphere specialization in processing of verbal and symbolic stimuli like letters and words (Dehaene & Cohen, 2011; Dien, 2009). This T1 asymmetry has also been previously reported (Śmigasiewicz et al., 2010), but is much smaller and not as easily replicable as the T2 asymmetry (Verleger & Śmigasiewicz, 2015).

A procedure similar but not identical to the present unilateral task was utilized by Verleger et al. (2009, Exp.2). In their experiment, T1 signaled spatial location of T2, thereby removing its uncertainty, but the target VF was still randomly varied trial-by-trial, and spatial and temporal locations of T1 always remained uncertain. Therefore, involvement of spatial attention was not as diminished, remaining at a controlled level during the whole trial, as in the present unilateral task. Moreover, providing information about T2 location during the trial additionally involved an endogenous shift of spatial attention (initiated after T1 onset). As a result, the LVF advantage, although reduced, was not completely abolished. Nevertheless, taking into account those procedural differences, the results of Verleger et al.'s (2009) exp. 2 and of the present experiments (as well as of Śmigasiewicz, Hasan, et al., 2017) are in agreement in showing that spatial uncertainty is the critical factor for the LVF advantage to occur.

A possible limitation of the present study is that our methodology may confound variations of spatial uncertainty and hemispheres: Spatial certainty implies processing of T2 by the same hemisphere as T1, and spatial uncertainty implies possible change between hemispheres from T1 to T2 processing. This issue should be addressed in future studies.

4.2. Lateralization of temporal processing

As we have pointed out in the introduction, there are results from studies on temporal discrimination and temporal order judgment (Funnell et al., 2003; Hilkenmeier et al., 2012; Matthews & Welch, 2015) suggesting that temporal attention might be more efficient in the RH than in the LH. However, results of the present experiments showed no effects of the lag manipulations on VF differences and no significant LVF advantage in the unilateral task, which argue against the proposed hypothesis. Possibly, there is no overall consistent lateralization of temporal attention and those particular aspects of this phenomenon

that are involved in target selection in RSVP are not lateralized. Yet, since no direct evidence for the RH advantage in temporal attention has been found, it seems more plausible that temporal attention is generally not lateralized to the RH, and the computations within the 'when' pathway in the right parietal lobe (Battelli et al., 2007) are not related to attentional selection, and thus the aforementioned asymmetry in temporal discrimination and temporal order judgment may be due to lateralization of perceptual, rather than attentional, processing in the 'when' pathway. This explanation may seem incongruent with studies showing that the LH has better temporal resolution of perceptual processing than the RH (Nicholls, 1996; Nicholls et al., 2002; Okubo & Nicholls, 2005), but it is simply plausible that different aspects of perceptual processing are oppositely lateralized. Also, the direction of lateralization of temporal processing may change dynamically, depending on specific task requirements, like transient detection or sustained monitoring (Okubo & Nicholls, 2008), or on task demands (Helton et al., 2010; Pérez et al., 2009).

Still, there is also the evidence mentioned in the Introduction showing involvement of the right IPS in temporal attention (Cooper et al., 2004; Husain et al., 1997; Marois et al., 2000). A plausible explanation of the incongruence between this evidence and the present results is that the right IPS is not the only essential node for target temporal selection in RSVP, and that other nodes of this mechanism are not right-lateralized, or even are left-lateralized, which may cancel out any hemispheric imbalance in terms of controlling temporal attention in the left and right VFs. There is evidence conforming to such an account. First, a lesion study by Shapiro, Hillstrom, and Husain (2002) has shown that another parietal structure, the inferior parietal lobe (IPL), is also critical for temporal target selection in RSVP and that damage of the left IPL disturbs this process similarly as damage of the right IPL. Second, an fMRI study by Kranczioch, Debener, Schwarzbach, Goebel, and Engel (2005) has shown that successful T2 selection during the blink period not only involved the right and left IPL, but also that the activation was significantly larger in the LH than in the RH. And third, a TMS study by Kihara et al. (2011) has suggested that while the IPS is generally related to selection of task-relevant targets, the IPS may be even more specifically related to successful deployment of temporal attention during the blink period, because it contributes to disengagement and temporal reorienting of attention from T1 to T2. (It should be mentioned here that successful target identification in RSVP tasks involves several mechanisms underlain by a large-scale network comprising, besides attentional selection localized in the parietal areas, also stimulus identification localized in the inferior temporal areas, and memory encoding localized in the lateral frontal areas; for reviews see: Hommel et al., 2006; Martens & Wyble, 2010.)

Interestingly, there are two published RSVP studies with split-brain patients (Giesbrecht & Kingstone, 2004; Ptito, Brisson, Dell'Acqua, Lassonde, & Jolicoeur, 2009) and both have reported a RVF advantage in T2 identification in patients, instead of the usual LVF advantage, and no VF asymmetry in normal healthy participants from control groups. This RVF advantage in patients might reflect a LH advantage in temporal attention, contrary to the hypothesized here RH advantage, or the aforementioned LH advantage in perceptual processing (Nicholls, 1996). It is unclear, however, how to interpret those results, because the procedures of the tasks used in both studies were generally similar to the present "standard" bilateral RSVP task, and it is therefore difficult to explain why such different results were obtained in those studies. (In these split-brain experiments, four simultaneous RSVP streams were presented, two in the LVF and two in the RVF, instead of the more usual two lateral streams, but the LVF advantage has been observed in the four-stream RSVP task as well, see: Exp.6 of Scaf, Banich, Kramer, Narechania, & Simon, 2007). Notwithstanding, the results both of the present experiments and of the two split-brain studies are unanimous in their lack of support for the hypothesis of RH advantage in temporal attention.

4.3. Lateralization of spatial attention

The notion of RH predominance in stimulus-driven spatial attention has solid empirical support. As mentioned in the Introduction, brain imaging studies have shown rather consistently that several main nodes of the network underlying stimulus-driven orienting are lateralized to the RH (de Haan, Bither, Brauer, & Karnath, 2015; Natale, Marzi, & Macaluso, 2010; Siman-Tov et al., 2007). One of the more recent fMRI studies by Shulman et al. (2010) has reliably demonstrated this asymmetry in a variant of the RSVP task with spatial cuing using a method of direct voxelwise comparisons of activity in left and right hemispheres. This evidence from neuro-imaging is extended by neuropsychological data, often showing deficits of spatial attention after lesions in the RH, but very rarely after lesions in the LH (Bartolomeo, 2014; Corbetta & Shulman, 2011), and by studies with transcranial magnetic stimulation (TMS) showing causal relations between the RH attention network and spatial orienting (Chambers, Payne, Stokes, & Mattingley, 2004; Heinen et al., 2011). Those brain studies are complemented by behavioral evidence of a LVF advantage observed in conditions involving exogenously triggered spatial orienting (Asanowicz, Marzecová, Jaśkowski, & Wolski, 2012; Du & Abrams, 2010; Evert, McGlinchey-Berroth, Verfaellie, & Milberg, 2003). Endogenous spatial attention, on the other hand, seems to be organized rather bilaterally, with essential nodes localized in the intraparietal sulcus and frontal eye field, providing similar capacity for both hemispheres (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Hopfinger, Buonocore, & Mangun, 2000; Luck, Hillyard, Mangun, & Gazzaniga, 1994; Shulman et al., 2010). The present study adds another data point to this line of research on dissociation and lateralization of endogenous and exogenous spatial orienting.

4.4. Lateralization of attention vs. lateralization of perception

The LVF advantage in the RSVP task might be due to lateralization of perceptual rather than attentional processing. First, recent ERP and fMRI studies have shown that while letters are processed in the LH's visual system, digits are actually preferentially processed in the RH's visual system (Park, Chiang, Brannon, & Woldorff, 2014; Park, Hebrank, Polk, & Park, 2012). Therefore, one might interpret the LVF advantage in identification of T2, which were digits in most of the reported studies, as an effect of this perceptual asymmetry. However, the LVF advantage has been observed also with different types of T2s, like Latin letters, geometrical shapes, and faces (Asanowicz et al., 2013, 2017). Second, it has been shown that the RH is generally more efficient than the LH at early cortical stages of visual processing (Grabowska & Nowicka, 1996; Hellige & Michimata, 1989; Hellige & Webster, 1979) which may be reflected in earlier latencies of distractor-evoked visual evoked potentials at the RH than at the LH (Asanowicz et al., 2017; Verleger et al., 2011, 2013). Thus far, however, there has been no evidence that this perceptual RH advantage is related, let alone causal, to the LVF advantage in T2 identification (Asanowicz et al., 2017; Śmigajewicz, Liebrand, Landmesser, & Verleger, 2017). In conclusion, this VF asymmetry does not seem to be due to lateralization of perceptual processing.

4.5. Relationship between temporal and spatial attention

There is discussion in the literature whether temporal and spatial components of perceptual and attentional processing are independent and how they may interact in performance (Battelli et al., 2007; Husain & Rorden, 2003; Rizzo, Akutsu, & Dawson, 2001; Rohenkohl, Gould, Pessoa, & Nobre, 2014). In this line, Husain et al. (1997) have found abnormally prolonged attentional blinks in patients with spatial neglect, and more recently, Li, Rorden, and Karnath (2017) have found that the magnitude of the attentional blink in neglect patients was

larger when stimuli were presented on their contralesional (i.e., left) than on their ipsilesional (i.e., right) side. Li and colleagues argue that this proves the interrelation between temporal and spatial processing and contradicts the hypothesis of their independence. Interestingly, results of the present study seem to provide evidence both against and for this hypothesis. On the one hand, the impact of spatial attention on the LVF advantage was not affected by variations of temporal parameters, which suggests independence of these two aspects of attention in terms of lateralization of performance. On the other hand, however, in Exp.1 we found that the effect of lag, i.e., the attentional blink, was largest when involvement of spatial attention was strongest, i.e., when in the bilateral task T1 and T2 occurred in opposite VFs, which suggests that temporal and spatial attention indeed may interact. Thus, a tentative conclusion would be that temporal and spatial attention may interact in some aspects of performance.

4.6. Mechanism underlying the LVF advantage

The present results suggest that the LVF advantage in the bilateral RSVP task reflects RH predominance in stimulus-driven spatial attention. However, a plausible mechanism of producing this unusually large asymmetry may also include two other aspects of visuo-spatial information processing: biased competition and interhemispheric transfer. Because in this task participants do not know where and when target stimuli will occur, identification of the targets requires constant monitoring of both simultaneous streams of distractors. This results in a competition between hemifields/hemispheres for attention, which is biased (cf. the biased competition model, Desimone & Duncan, 1995), because the spatial attention system is lateralized to the RH. The RH selection system has a direct access to LVF information, whereas the RVF information has yet to be relayed to the RH through the corpus callosum, which takes more time and the transfer process may also degrade the relayed information (cf. the callosal relay model of functional lateralization, Moscovitch, 1986; Zaidel, 1983). Acting together, these factors appear to produce a process that strongly favors LVF information over RVF information and results in this unusually large and stable LVF advantage.

4.7. Conclusion

The present study investigated whether the LVF advantage in T2 identification, as observed in a bilateral RSVP task, reflects lateralization of temporal attention or of spatial attention. Involvement of temporal attention was manipulated by changing T1-T2 lag intervals, from least (lag 8) to moderate (lag 4) and to most (lag 2) involvement, yet this manipulation did not affect VF asymmetry. Moreover, no significant LVF advantage was found when involvement of stimulus-driven spatial attention was eliminated (unilateral task with no spatial uncertainty, Exp.1 & 2), whereas the usual LVF advantage was observed when stimulus-driven spatial attention was involved (bilateral task with spatial uncertainty, Exp.1). This adds to the conclusion that the LVF advantage does not reflect lateralization of temporal attention, but rather predominance of the right hemisphere in spatial orienting, and suggests that temporal attention may not be lateralized.

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